

# Species associations of congeneric species in a tropical seasonal rain forest of China

Guoyu Lan<sup>\*,†</sup>, Yunbing Zhang<sup>\*</sup>, Fangliang He<sup>‡</sup>, Yuehua Hu<sup>\*</sup>, Hua Zhu<sup>\*</sup> and Min Cao<sup>\*,1</sup>

<sup>\*</sup> Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, 88 Xuefu Road, Kunming 650223, P. R. China

<sup>†</sup> Rubber Research Institute, The Chinese Academy of Tropical Agricultural Sciences, Danzhou City, Hainan Province, 571737, P. R. China

<sup>‡</sup> Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada T6G 2H1

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**Abstract:** In tropical plant communities with diverse species, many congeners are found to coexist. Do environment or biotic interactions structure the coexistence of congeners in tropical forest communities? In this paper, we aimed to disentangle the effect of environment (first-order effects) and species interactions (second-order effects) on the spatial distributions of tree species. We used a classification scheme and torus-translation to test the first-order interaction of 48 species from 17 genera in a fully mapped 20-ha dipterocarp tropical seasonal rain-forest plot in Xishuangbanna, south-west China. Then we used heterogeneous Poisson null models to reveal significant uni- and bivariate second-order interactions. The results demonstrated that (1) 34 of the 48 studied species showed a significant relation with at least one topographic variable. This confirmed that topographical heterogeneity is important for distribution of these congeners. Spatial segregation (36.6%) and partial overlap (34.8%) were the most common bivariate association types in Xishuangbanna plot, which indicated first-order effects (environment) were strong. (2) For small-scale associations, 51% saplings (1 to ≤ 5 cm) (68.8% for large trees with dbh > 5 cm) of the species showed non-significant associations. For large-scale associations, 61.6% saplings (81.2% for large trees) of the species showed non-significant associations. Lack of significant species interactions provides evidence for the unified neutral theory. In conclusion, both environment and biotic interactions structure congeneric species' coexistence in tropical seasonal rain forest in this region.

**Key Words:** congeners, neutral theory, spatial segregation, species-habitat association, Xishuangbanna

## INTRODUCTION

Numerous mechanisms have been proposed to explain coexistence of tree species in tropical forests at local scales (Wright 2002). Niche differentiation with respect to resources remains a prominent hypothesis to account for the maintenance of tree species diversity in tropical forests (Harms *et al.* 2001). However, mechanisms based on neutral theories, where ecological drift is the main force structuring species-rich communities, and speciation is one of the stochastic processes involved in this drift (Hubbell 2001), can also form patterns of distribution and abundance similar to those found in nature (Chave 2004, Mouquet & Loreau 2003, Purves & Pacala 2005).

Congeners may utilize a similar set of resources in a similar way (Ackerly & Donoghue 1998, Mooney *et al.* 2008) if traits are phylogenetically conserved

among species in a particular plant community (Ashton *et al.* 2004, Swenson *et al.* 2007) and experience relatively intense interspecific competition that limits their coexistence (Mooney *et al.* 2008, Webb *et al.* 2002). Many congeners are found to coexist in both tropical forest and temperate forest (Davies *et al.* 1998, Queenborough *et al.* 2007, Tanaka *et al.* 2008). Davies *et al.* (1998) compared 11 species of *Macaranga* (Euphorbiaceae) in a tropical rain forest in Borneo, and concluded that heterogeneity of resource availability resulted in differences in tree distribution, which is important for their coexistence. However, Queenborough *et al.* (2007) compared 16 species of Myristicaceae in a tropical rain forest in Amazonian Ecuador, and found no evidence that partitioning of physical habitats could explain the coexistence of all 16 closely related species.

Previous studies using principal coordinates neighbour matrices (PCNM) method shows that topography can explain more than 20% of the total variation of dominant species abundance in tropical seasonal rain forest in

<sup>1</sup> Corresponding author. Email: langyri@163.com, caom@xtbg.ac.cn

Xishuangbanna, south-west China (Lan *et al.* 2011), which gives support for niche partitioning in facilitating species coexistence in this tropical forest. However, we still have no idea about how topography (first-order effects) affects the distribution pattern of congeners. Lan *et al.* (2012) found that it is notable that a high number of positive associations were found in dominant species. An interesting question is therefore how often do two congeneric species show positive association at scales above the typical scale at which plant-plant interactions (second-order effects) occur. Our objective is finding evidence that both environment and biotic interactions are facilitating coexistence of congeneric species in tropical seasonal rain forest in Xishuangbanna. We tested the hypotheses that both niche partitioning and stochastic (i.e. neutral) processes could play an important role in structuring the coexistence of congeneric species in this region.

## METHODS

### Study site

The study site was located in the Xishuangbanna National Nature Reserve in Yunnan province, south-west China (101°34'E, 21°36'N). Xishuangbanna is included in the Indo-Burma biodiversity hotspot and contains over 5000 species of vascular plant, comprising 16% of China's total plant diversity (Cao & Zhang 1997, Myers 1988). The tropical seasonal rain forest in Xishuangbanna, is the most important vegetation type and harbours biodiversity that is important both for global and national species richness in China. This region is dominated by a typical monsoon climate with an alternation between a dry season and a rainy season. The mean annual temperature is 21.0°C, and the mean annual precipitation is 1532 mm, of which approximately 80% occurs between May and October.

### Data collection

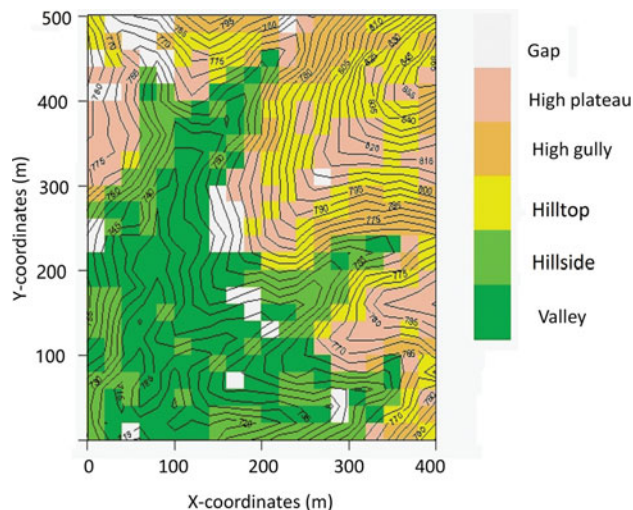
A 20-ha permanent forest plot was established in the Xishuangbanna National Nature Reserve in 2007 following the field protocol of the Center for Tropical Forest Science and Forest Global Earth Observatories (CTFS-ForestGEO) (Condit 1998). The plot measures 400 m (north-south) by 500 m (east-west). The altitude ranges from 709 m to 869 m asl with a mean of 765 m asl; the highest altitude occurs in the north-west corner of the plot. The forest occurs mainly on laterite and lateritic red soils with pH values ranging from 4.5 to 5.5 (Zhu 2006). All trees ( $\geq 1$  cm in diameter at breast height, dbh) were mapped and tagged with unique numbers. The emergent layer consists largely of the species *Parashorea*

*chinensis* Hsie Wang; the main canopy layer, contains trees up to 30 m high with almost continuous crowns and is dominated by *Sloanea tomentosa* (Benth.) Rehd. & Wils., *Pometia tomentosa* (Bl.) Teysm. & Binn., *Semecarpus reticulata* Lect. and *Barringtonia pendula* (Griff.) Kurz (Lan *et al.* 2012, Zhu 2006).

We selected the top 48 tree species with the largest number of individuals for our analysis. And these species comprised more than 24.5% of the total individuals (95 498) and 26.0% of the total basal area (835 m<sup>2</sup>) of trees  $\geq 1.0$  cm dbh. Species abbreviations are shown in Appendix 1. In order to investigate the species distribution patterns and how the species associations change across life stages, we classified the individuals of each species into the two life stages: saplings (1 to  $\leq 5$  cm dbh) and large trees ( $> 5$  cm dbh).

### Species habitat association

Three topographic attributes were measured in the field: altitude, slope and convexity for the 20 × 20-m cells. Following Harms *et al.* (2001), altitude of a cell was defined as the mean of the altitude values at its four corners. Convexity was the altitude of the cell of interest minus the mean altitude of the eight surrounding cells. For the edge cells, convexity was the altitude of the centre point minus the mean of the four corners (Legendre *et al.* 2009). We divided the habitat into six types, namely: (1) valley (slope  $< 27.1^\circ$ ; altitude  $< 765$  m asl), (2) hillside (slope  $> 27.1^\circ$ ; altitude  $< 765.0$  m asl), (3) hilltop (slope  $\geq 27.1^\circ$ ; altitude  $\geq 765$  m asl, convexity  $> 0$ ), (4) high-gully (slope  $\geq 27.1^\circ$ ; altitude  $\geq 765$  m asl, convexity  $< 0$ ), (5) high-plateau (slope  $< 27.1^\circ$ ; altitude  $\geq 765$  m asl, convexity  $> 0$ ) and (6) gap (with a total open area greater than 200 m<sup>2</sup>) (Figure 1). In order to control for the effects of dispersal limitation, we used torus-translation tests (Harms *et al.* 2001) to assess potential association of the spatial patterns of species with different topographic habitats. The tests assess the similarity between the spatial structure of each focal species population and each habitat. For each species, the observed relative densities of stems in each of the habitats were compared with expected relative densities. To obtain the expected values, the true habitat map was shifted about a two-dimensional torus by 20-m increments to exhaustively produce all possible 20-m translations of the true habitat map in the four cardinal directions. Each of the 500 maps provided an estimate of the expected relative density. A species was significantly positively associated with a particular habitat if its relative density in the true habitat map was  $> 97.5\%$  of the values obtained from translated maps. A significant negative association occurred if the relative density in the true map was  $< 97.5\%$  of the values from translated maps. We used



**Figure 1.** Habitat of the 20-ha permanent plot of tropical seasonal rain forest in Xishuangbanna, south-west China. Valley: slope < 27.1°, altitude < 765 m asl; Hillside: slope > 27.1°, altitude < 765 m asl; hilltop: slope ≥ 27.1°, altitude ≥ 765 m asl, convexity > 0; High-gully: slope ≥ 27.1°, altitude ≥ 765 m asl, convexity < 0; High-plateau: slope < 27.1°, altitude ≥ 765 m asl, convexity > 0; Gap: with a total open area greater than 200 m<sup>2</sup>.

the 161 tree species with a density ≥ 66 individuals for the torus-translation tests.

### Classification scheme of large-scale first-order association

First-order effects caused by specific habitat associations mediate second-order effects caused by intraspecific and interspecific associations. So, we used a simple scheme to classify first-order association of bivariate heterogeneous patterns (Wiegand *et al.* 2007). The distribution function  $P_{12}(n, r)$  that gives the probability of finding  $n$  trees of species 2 within neighbourhoods of radius  $r$  around trees of species 1, which can be used to describe the spatial association between two species. If the point configurations between pairs of trees of the two species are the same all over the study plot except for stochastic variation (i.e. homogeneous patterns), the mean of  $P_{12}(n, r)$  with respect to  $n$  suffices, which is given by  $\lambda_2 K_{12}(r)$ . The same value of the mean (i.e.  $\lambda_2 K_{12}(r)$ ) may arise for substantially different situations, e.g. if (1) all trees of species 1 have more or less the same number of neighbours of species 2 (i.e. a homogeneous pattern) or if (2) a few trees of species 1 have many species-2 neighbours but many trees of species 1 have no species-2 neighbours (an extremely heterogeneous pattern). We selected the value of the distribution  $P_{12}(n, r)$  at  $n = 0$  as an additional summary statistic.  $P_{12}(n = 0, r)$  is the probability that a tree of species 1 has within distance  $r$  no neighbour of species 2, i.e.  $P_{12}(n = 0, r) = 1 - D_{12}(r)$ . Because the summary statistics  $K_{12}(r)$  and  $D_{12}(r)$  express

fundamentally different properties of bivariate point patterns, they are a good choice for classifying different types of bivariate association. The expectations of the two summary statistics under the null model yield  $D_{12}^{exp} = 1 - \lambda_2 \pi r^2$  and  $K_{12}^{exp}(r) = \pi r^2$ , where the 'exp' superscript indicates expected by the null model of no spatial patterning. The two axes of the scheme are defined as:

$$\hat{P}(r) = \hat{D}_{12}(r) - (1 - \lambda_2 \pi r^2), \quad M(r) = \ln \left( \frac{\hat{K}_{12}(r)}{\pi r^2} \right) \quad (1)$$

We subtracted the theoretical values under the null model to move null association onto the origin of the scheme (i.e. no departure from the null model) and log-transformed the K-function in order to weight positive or negative departures from the null model in the same way. The scheme allows four different types of bivariate associations (Wang *et al.* 2010, Wiegand *et al.* 2007). The two patterns are segregated for  $\hat{M}(r) < 0$  and  $\hat{P}(r) < 0$  (segregation, type I). For  $\hat{M}(r) < 0$  and  $\hat{P}(r) > 0$ , the association is characterized by partial overlap (type II). For  $\hat{M}(r) > 0$  and  $\hat{P}(r) > 0$ , the two patterns occur within the same area (mixing; type III). There is a fourth type ( $\hat{M}(r) > 0$  and  $\hat{P}(r) < 0$ ). Type-IV associations will rarely occur (Wiegand *et al.* 2007). More details can be obtained from Wiegand *et al.* (2007) and Wang *et al.* (2010).

### Univariate plant–plant interaction

To reveal significant second-order effects in the univariate patterns (i.e. regularity and aggregation), we constructed the intensity function  $l(x, y)$  based on the pattern of the species under study and selected for all 48 species a bandwidth  $h = 30$  m. This scale is slightly larger than typical scales at which local point-point interactions have been reported in tropical forests (Hubbell *et al.* 2001, Peters 2003), but it is smaller than the range over which the environmental gradients may vary (Harms *et al.* 2001, John *et al.* 2007). We studied plant–plant interactions with a spatial resolution of 2 m up to 30 m.

### Bivariate plant–plant interaction

To reveal significant second-order effects in the bivariate patterns (i.e. repulsion and attraction), we kept the location of the trees of the first species fixed and randomized the locations of the trees of the second species using a heterogeneous Poisson null model. Here the intensity function  $l_2(x, y)$  was constructed based on pattern 2.

Again, we used a bandwidth  $h = 30$  m and a spatial resolution of 2 m. This null model allowed us to assess whether pattern-2 points were more or less frequent around pattern-1 points than expected by the intensity of pattern 2, which would indicate attraction or repulsion,

respectively. Note that we tested all pairs, that is, species 1 versus species 2 and species 2 versus species 1, since we cannot assume that the interaction will be symmetric (Vázquez *et al.* 2007).

### Large-scale interspecific spatial associations

We used the null hypothesis that species 2 followed the intensity of species 1. The corresponding null model was again a heterogeneous Poisson null model where the locations of the trees of species 1 were fixed, but the locations of the trees of the second species were randomized in accordance with the intensity of species 1. In this analysis, we used a bandwidth of  $h = 50$  m to estimate the intensity of species 1 and a spatial resolution of 5 m because we were interested only in larger-scale effects.

We performed 199 Monte Carlo simulations of the null model and used the fifth-lowest and fifth-highest simulated  $g(r)$  values as simulation envelopes. The 199 simulations generated sufficiently smooth simulation envelopes. Significant departure from the null model occurred at scale  $r$  if the empirical pair correlation function was outside the simulation envelopes. These simulations were used for all analyses and all analyses were performed using the Programita software (Wiegand & Moloney 2004).

## RESULTS

### Species-habitat association

The torus-translation tests revealed that 34 of 48 (70.8%) species were either positively or negatively associated with at least one habitat (Appendix 2). For species association, there was a total of 112 congeneric species pairs among the 48 species. However, 10 (8.9%) of the total 112 species pairs shared similar habitats (Appendix 2). Both *Castanopsis echidnocarpa* and *Castanopsis hystrix* were negatively associated with hillside, but positively associated with high plateau. However, most congener pairs (103, 91.1%) did not share similar habitats. For example, *Castanopsis indica* was positively associated with valley and hillside, and negatively associated with hilltop and high plateau. However, *Castanopsis mekongensis* negatively associated with hillside and gap, and positively associated with high plateau. *Litsea baviensis* was negatively associated with hillside. Whereas, *Litsea dilleniifolia* was positively associated with valley and negatively associated with hilltop.

### Classification scheme of bivariate associations

The various types of non-random effect in interspecific association were not equally distributed among the

112 species pairs analysed, and their relative frequency depended on scale (Appendix 3). The most notable result is that roughly half of the species pairs showed segregation at all three spatial scales analysed (55, 42 and 40 cases at scales of 5, 30 and 50 m, respectively). Thus, trees of different species co-occur less often than expected by chance. Interestingly, partial overlap was rare in the 5-m neighbourhood (eight cases), but more frequent in the 30-m and 50-m neighbourhoods (39 and 37 cases, respectively). Mixing occurred in 47 cases at the 5-m scale but only 27 and 20 times at the 30-m and 50-m scales respectively. For example, *C. echidnocarpa* and *C. mekongensis* were distributed together (mixing association), however, *L. dilleniifolia* and *Litsea garrettii* were segregated in the plot (segregation association) (Figure 2).

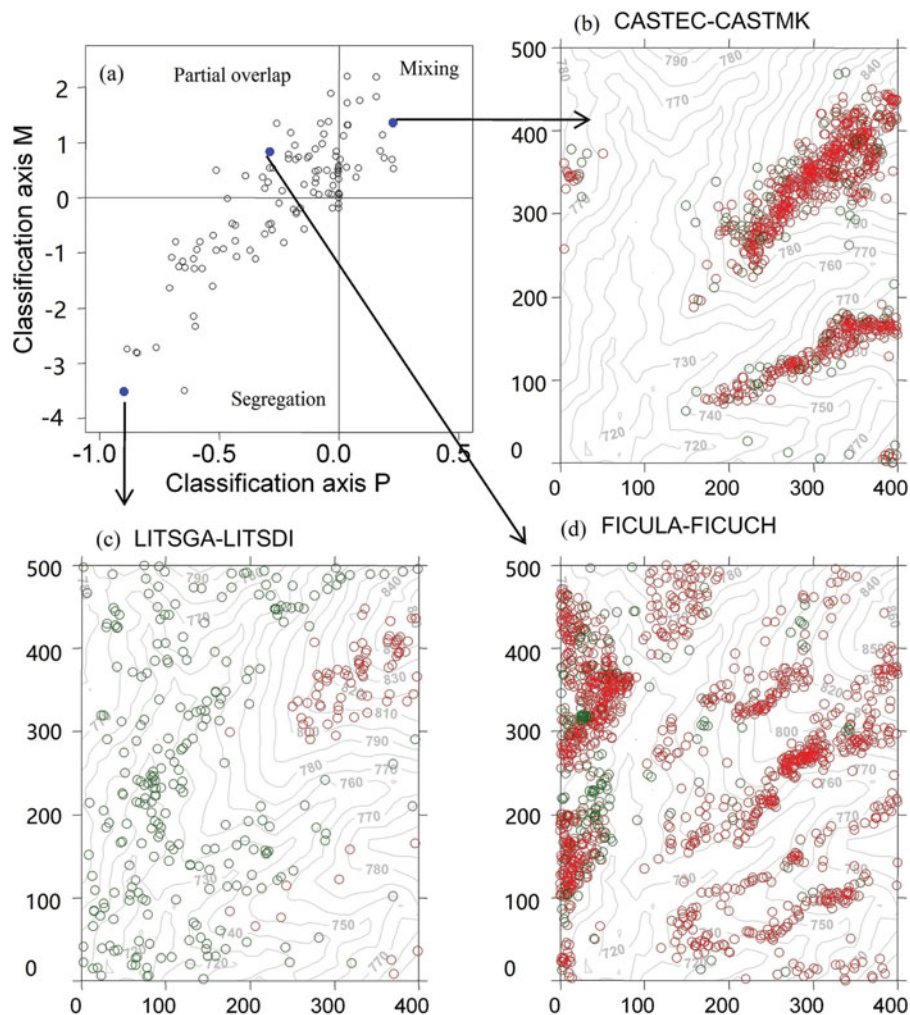
### Species distribution patterns

We performed a total of 96 univariate point pattern analyses for the 48 species in 17 genera across size classes (Appendix 2, Figure 3a, b). For saplings with dbh < 5 cm, 46 of total species aggregated at scales 0–10 m, however, only two species (*Ficus auriculata* and *Garcinia xanthochymus*) showed random distribution pattern at such scales. However, 38 (79.2%) species (large trees) showed an aggregated distribution pattern at scales 0–10 m, and 10 (20.8%) species had a random distribution pattern. Generally speaking, more species showed aggregated distribution pattern than random distribution pattern at scales 0–10 m, and vice versa at scales larger than 10 m. Figure 4 shows the examples of distribution maps and spatial distribution pattern of univariate patterns.

### Species associations

For small-scale associations, we performed a total of 224 tests of species pairs among 48 species (Figure 3). For saplings, a total of 37 (33.0%) pairs of congeneric species were positively associated (attraction) at a scale of 0–5 m, however 18 (16.1%) species pairs were negatively associated (repulsion) at this scale. For large trees, a total of 22 (19.6%) species pairs were positively associated at 0–5 m, and 13 (11.6%) species pairs were negatively associated at this scale.

For large-scale association, we also performed a total of test of 224 species pairs. The results showed that a total of 29 (25.9%) pairs of congeneric species among saplings were positively associated (attraction) at the scale of 0–5 m, however 14 (12.5%) species pairs were negatively associated (repulsion) at this scale. For large trees, a total of 15 (13.4%) species pairs were positively associated, and 6 (5.4%) species pairs were negatively associated at this scale. Figure 5 shows examples for significant small-scale



**Figure 2.** Classification of large-scale associations at a 30-m scale in the tropical seasonal rain forest in Xishuangbanna, south-west China. The allocation of the large-scale association of the 112 species pairs based on the classification axes (a). Examples for type III association with mixing (b), type I association with segregation (c) and type II association with partial overlap (d). Red open circle: species 1, green open circle: species 2.

and large-scale interactions between *Diospyros hasseltii* and *D. nigrocortex*.

## DISCUSSION

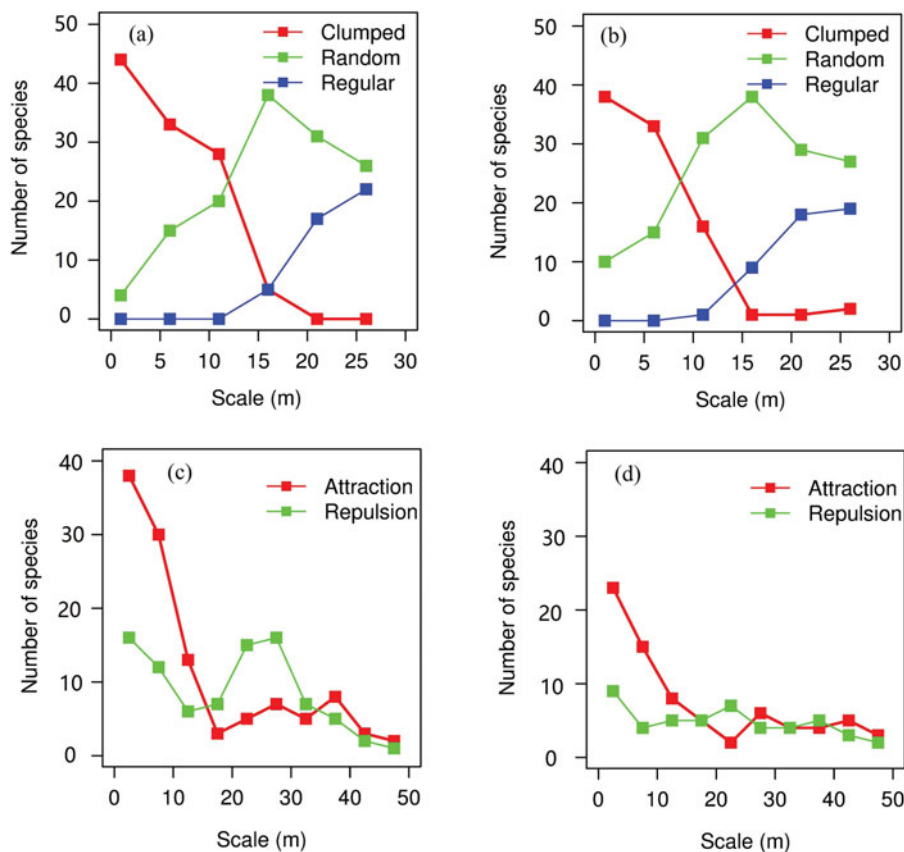
### Species habitat association

The topography of our site was very complex. In our plot, species habitat association test shows that 34 of the 48 studied species showed a significant relationship with at least one of the topographic variables. Our results further confirmed the results of Davies *et al.* (1998) that heterogeneity is important for the coexistence of congeners. In other words, the present study provides evidence of niche partitioning operating in congeners in a tropical seasonal rain forest. We also compared the results of torus translation of species habitat associations and found that 10 (8.9%) of the total species pairs shared

similar habitats (Appendix 2), both *C. echidnocarpa* and *C. hystrix* were negatively associated with hillside, and *L. baviensis* and *L. garrettii* also were negatively associated with hillside, which would indicate that some congener traits are phylogenetically conserved (see growth type and fruit type in Appendix 1).

### Classification scheme of bivariate associations

We found that all 45 (93.8%) species were significantly aggregated and that spatial segregation (36.6%) and partial overlap (34.8%) were the most common bivariate association types at the Xishuangbanna plot, which indicated first-order effects were strong (Wiegand *et al.* 2007) and gives support for niche partitioning in facilitating species coexistence. However, the percentage of mixing was 15.2%, which was much higher than a tropical forest in Sri Lanka (5.4% in Sri Lanka) (Wiegand



**Figure 3.** Number of species (univariate) and species-species pairs (bivariate) where the observed pair-correlation function is for a given scale  $r$  outside the Monte Carlo simulation envelopes, being the fifth-lowest and fifth-highest values of the simulated  $g(r)$  of the 20-ha permanent plot of tropical seasonal rain forest in Xishuangbanna, south-west China. Univariate analyses of saplings (a); Univariate analyses of large trees (b); Small-scale bivariate analyses of saplings (c). Small-scale bivariate analyses of large trees (d).

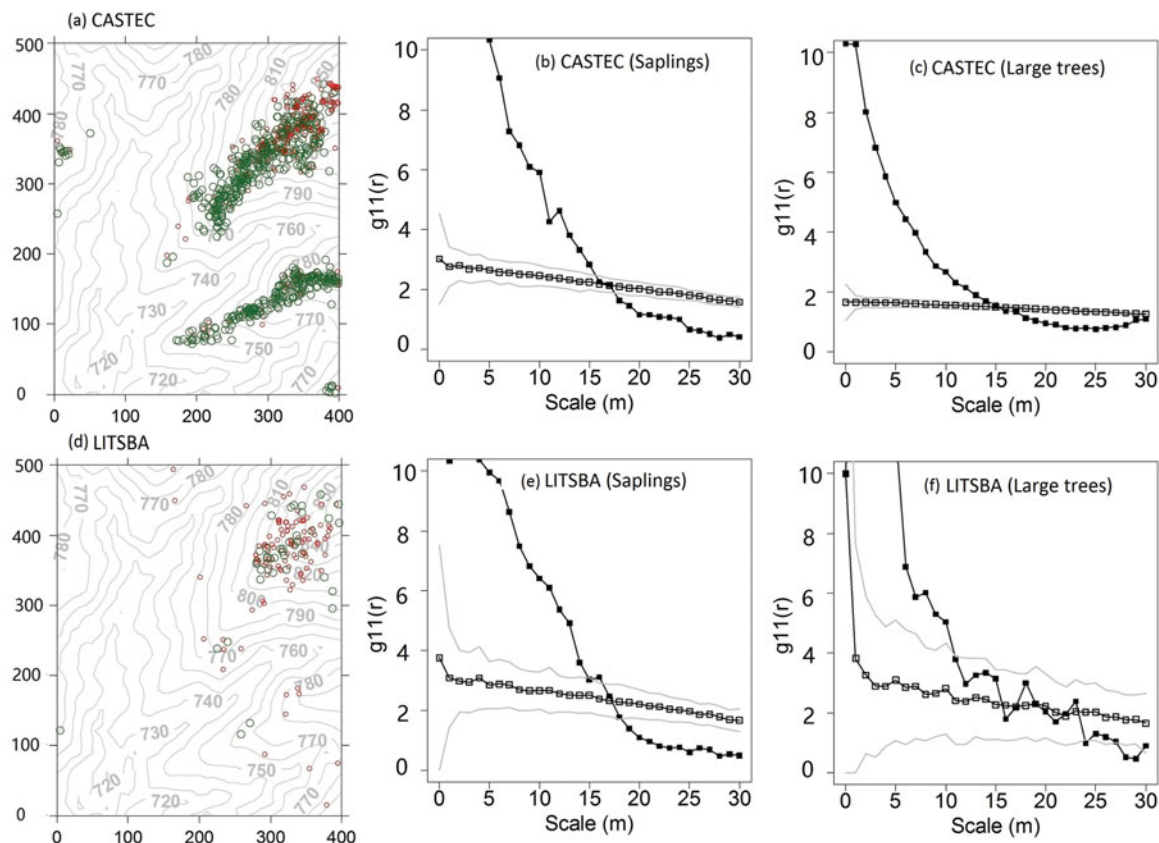
*et al.* 2007). In particular, at scale 0–5 m there were 42 (37.5%) species pairs of mixing association. This also confirmed that some congeners may share similar habitats as stated above.

### Spatial distribution pattern

The present study showed that aggregated patterns were also found for both saplings and large trees. This result is in accordance with the findings of many other studies (Condit *et al.* 2000, He *et al.* 1997, Henriques & Desousa 1989). Aggregated distributions may result from limited seed dispersal (Grubb 1977) or habitat heterogeneity (Harms *et al.* 2000, Queenborough *et al.* 2007). It is worth noting that some saplings did not aggregate more densely than larger trees. For example, saplings of *Litsea pierrei* had a random distribution pattern, while large trees had an aggregated distribution pattern. Species in which larger trees were more densely aggregated than juveniles are also suggestive of habitat-related patchiness, because adults might be collected in sites most favourable for the

species, whereas juveniles are widely dispersed (Condit *et al.* 2000). This further confirmed that heterogeneity is important for distribution patterns of these congeners.

However, the positive or negative associations to the topographic habitats are more likely to cause larger-scale aggregation which was approximately factored out by the heterogeneous Poisson null model (Lan *et al.* 2012). Thus, other factors may be responsible for the strong small-scale clustering of saplings. For the genus *Castanopsis*, limited seed dispersal is considered the most likely explanation. In the present study, the congeneric *Castanopsis* species disperse their seeds by rodents (Wang *et al.* 2004, Zhang *et al.* 2006). However, *Litsea* species may disperse their seeds by birds, which would contribute to the explanation of random distribution pattern at large-scale. Species whose seeds were dispersed by animals were assumed to be better dispersed than wind- or explosively dispersed species (Condit *et al.* 2000, Seidler & Plotkin 2006), this is why some saplings had random distribution pattern. Also, congeneric species may coexist within a community by adopting different regeneration niches (Yamada *et al.* 2005). Canopy trees were assumed to have well-dispersed



**Figure 4.** Examples of distribution maps and spatial distribution pattern of univariate patterns (two species: *Castanopsis echidnocarpa* and *Litsea baviensis*) in the 20-ha permanent plot of tropical seasonal rain forest in Xishuangbanna, south-west China. Shown are the univariate  $g_{11}$  pair-correlation functions of the data in dependence on scale  $r$  (solid squares) and the simulation envelopes (solid lines) of the Monte Carlo simulations of the null modes. Monte Carlo confidence was constructed at approximately 95% confidence level (199 simulations). See Appendix 1 for species codes. Red open circle is saplings ( $1 \leq 5$  cm dbh), and green open circle is large trees ( $> 5$  cm dbh). Distribution map of *C. echidnocarpa* (a); Univariate analyses of saplings of *C. echidnocarpa* (b); Univariate analyses of large trees of *C. echidnocarpa* (c); Distribution map of *L. baviensis* (d); Univariate analyses of saplings of *L. baviensis* (e); Univariate analyses of large trees of *L. baviensis* (f).

seeds relative to understorey treelets (Condit *et al.* 2000), this could be a possible reason why the saplings of canopy species *L. pierrei* have a random distribution pattern, while the saplings of the treelet *Litsea verticillata* showed a significant aggregated distribution pattern.

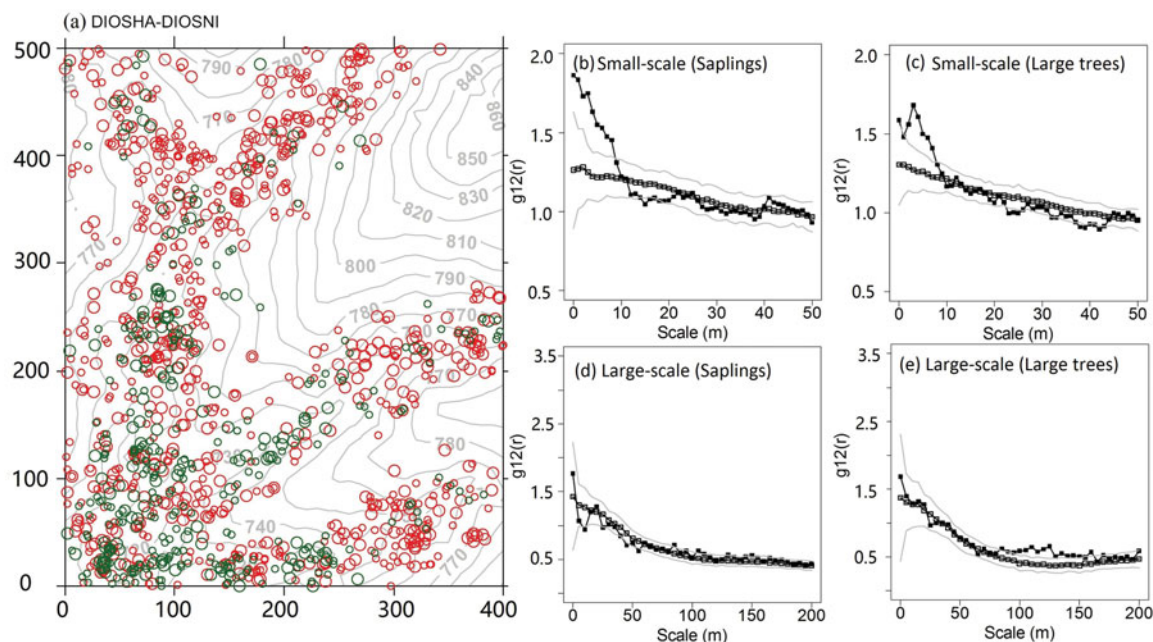
### Species association of congeners

Neutral theory assumes that species are ecologically equivalent in their responses to all constraints and thus have no interspecific trade-offs (Hubbell 2001); it predicts that high species diversity could result from a balance between speciation and stochastic extinction caused by random drifts in population size (Hubbell 2001). Interestingly, we found that 51% of saplings of the species showed non-significant associations (68.8% for large trees). For large-scale associations, for saplings 61.6% of the species had non-significant associations (neither positive nor negative). For large trees the proportion is

even greater at 81.2%. These proportions coincide with those shown in former studies such as those of Lieberman & Lieberman (2007), Wiegand *et al.* (2012) and Velázquez *et al.* (2015), and suggest that stochastic (i.e. neutral) processes could play an important role in structuring this community.

The storage effect is a stochastic mechanism of coexistence, which also could produce the stochastic patterns (Chesson 1984). In nature, environments vary substantial in time. Some of the variation is regular, some of it is stochastic. Environmental variation can contribute to coexistence if species have different competitive abilities under different microhabitat conditions (Sears & Chesson 2007).

In conclusion, our results show heterogeneity is important for the coexistence of congeners, which provides evidence of niche partitioning operating in congeners in a tropical seasonal rain forest. A large proportion of species showed non-significant associations, and suggests that stochastic (i.e. neutral) processes could



**Figure 5.** Examples for significant small-scale interactions and large-scale interactions across size class of the 20-ha permanent plot of tropical seasonal rain forest in Xishuangbanna, south-west China. Shown are the bivariate  $g_{12}$  pair-correlation functions of the data in dependence on scale  $r$  (solid squares), and the expected  $g_{12}(r)$  function under the heterogeneous Poisson null model (open squares) and the Monte Carlo simulation envelopes (solid lines) of the null models. Monte Carlo confidence was constructed at approximately 95% confidence level (199 simulations). See Appendix 1 for species codes. Red small open circle: saplings ( $\text{dbh} \leq 5$ ) of *Diospyros hasseltii*; Red large open circle: large trees ( $\text{dbh} > 5$ ) of *D. hasseltii*; Green small open circle: saplings ( $1 \leq \text{dbh} \leq 5$ ) of *Diospyros nigrocortex*; Green large open circle: large trees ( $\text{dbh} > 5$ ) of *D. nigrocortex*. Distribution map of *D. hasseltii* and *D. nigrocortex* (a); Small-scale bivariate analyses of saplings of *D. hasseltii* and *D. nigrocortex* (b); Small-scale bivariate analyses of large trees of *D. hasseltii* and *D. nigrocortex* (c); Large-scale bivariate analyses of saplings of *D. hasseltii* and *D. nigrocortex* (d); Large-scale bivariate analyses of large trees of *D. hasseltii* and *D. nigrocortex* (e).

play an important role in structuring this community. In short, both environments and biotic interactions structure congeneric species coexistence in tropical seasonal rain forest in Xishuangbanna, south-west China.

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**Appendix 1.** Species properties of the 48 species in 17 genera in the 20-ha permanent plot of tropical seasonal rain forest in China. Treelets include all species with adults generally less than 10 m tall; understorey trees are those with adults 10–20 m tall; lower canopy species have heights of 20–30 m; and upper canopy species are those often 30–45 m in height and emergent above the main canopy (> 45 m). Information on the heights of the tree species was from Zhu (2006). Saplings (1 to ≤ 5 cm dbh), large trees (> 5 cm dbh).

Species	Family	Code	Abundance	Growth type	Fruit type	Basal area (m <sup>2</sup> )
<i>Alphonsea hainanensis</i> Merr. & Chun	Annonaceae	ALPHHA	96	Understorey	Berry	0.37
<i>Alphonsea monogyne</i> Merr. & Chun	Annonaceae	ALPHMO	143	Understorey	Berry	1.58
<i>Antidesma japonicum</i> Siebold & Zucc.	Euphorbiaceae	ANTIJA	275	Treelet	Drupe	1.03
<i>Antidesma montanum</i> Blume	Euphorbiaceae	ANTIMO	455	Understorey	Drupe	1.15
<i>Ardisiaquin quegona</i> Blume	Myrsinaceae	ARDIQU	211	Treelet	Capsule	0.52
<i>Ardiasio lanacea</i> Roxb	Myrsinaceae	ARDISO	331	Treelet	Capsule	1.99
<i>Beilschmiedia robusta</i> C.K. Allen	Lauraceae	BEILRB	120	Lower canopy	Berry	0.40
<i>Beilschmiedia roxburghiana</i> Nees	Lauraceae	BEILRX	468	Understorey	Berry	1.40
<i>Canarium subulatum</i> Guill.	Burseraceae	CANASU	188	Upper canopy	Drupe	1.00
<i>Canarium tonkinense</i> Leenh. Engl.	Burseraceae	CANATO	202	Understorey	Drupe	3.62
<i>Castanopsis echidnocarpa</i> Hook. f. & Thomson ex Miq.	Fagaceae	CASTEC	881	Low canopy	Nut	48.60
<i>Castanopsis hystrix</i> Miq.	Fagaceae	CASTHY	244	Low canopy	Nut	18.90
<i>Castanopsis indica</i> (Roxburgh ex Lindl.) A. DC.	Fagaceae	CASTIN	351	Low canopy	Nut	10.97
<i>Castanopsi smegaphylla</i> Hu	Fagaceae	CASTMG	255	Low canopy	Nut	18.24
<i>Castanopsis mekongensis</i> A. Camus	Fagaceae	CASTMK	108	Low canopy	Nut	3.62
<i>Diospyros hasseltii</i> Zoll.	Ebenaceae	DIOSHA	815	Treelet	Berry	12.47
<i>Diospyros nigrocortex</i> C.Y. Wu	Ebenaceae	DIOSNI	385	Understorey	Berry	2.45
<i>Elaeocarpus austroyunnanensis</i> Hu	Elaeocarpaceae	ELAEAU	162	Lower canopy	Drupe	2.37
<i>Elaeocarpus glabripetalus</i> var. <i>alatus</i> Kunth Hung T. Chang	Elaeocarpaceae	ELAEGL	170	Understorey	Drupe	5.74
<i>Elaeocarpus rugosus</i> Roxburgh	Elaeocarpaceae	ELAEERU	111	Lower canopy	Drupe	1.40
<i>Elaeocarpusv arumia</i> Buch.-Ham.	Elaeocarpaceae	ELAEVA	149	Lower canopy	Drupe	1.47
<i>Ficus auriculata</i> Lour.	Moraceae	FICUAU	115	Treelet	Achene	1.60
<i>Ficus chrysocarpa</i> Reinw.	Moraceae	FICUCH	178	Treelet	Achene	0.28
<i>Ficus fistulosa</i> Reinw. ex Blume	Moraceae	FICUFI	783	Treelet	Achene	0.57
<i>Ficus langkokensis</i> Drake	Moraceae	FICULA	1337	Understorey	Achene	7.64
<i>Garcinia cowa</i> Roxb.	Guttiferae	GARCCO	4333	Understorey	Berry	19.24
<i>Garcinia lancilimba</i> C.Y. Wu ex Y.H. Li	Guttiferae	GARCLA	618	Treelet	Berry	0.80
<i>Garcinia xanthochymus</i> Hook. f. ex T. Anderson	Guttiferae	GARCXA	102	Understorey	Berry	0.72
<i>Horsfieldia glabra</i> Reinw. ex Blume Warb.	Myristicaceae	HORSGL	132	Treelet	Drupe	0.61
<i>Horsfieldia pandurifolia</i> Hu	Myristicaceae	HORSPA	101	Lower canopy	Drupe	2.41
<i>Knema furfuracea</i> Hook. f. and Thomson Warb.	Myristicaceae	KNEMFU	3160	Lower canopy	Capsule	11.24
<i>Knema globularia</i> Lam. Warb.	Myristicaceae	KNEMGL	614	Understorey	Capsule	1.54
<i>Litsea baviensis</i> Lecomte	Lauraceae	LITSBA	153	Understorey	Drupe	0.63
<i>Litsea dillenii</i> P.Y. Pai & P.H. Huang	Lauraceae	LITSDI	260	Low canopy	Drupe	9.55
<i>Litsea garrettii</i> Gamble	Lauraceae	LITSGA	86	Understorey	Drupe	0.37
<i>Litsea panamanja</i> (Nees) Hook. f.	Lauraceae	LITSPA	66	Low canopy	Drupe	1.86
<i>Litsea pierrei</i> var. <i>szemois</i> H. Liu	Lauraceae	LITSPI	114	Low canopy	Drupe	4.32
<i>Litsea verticillata</i> Hance	Lauraceae	LITSVE	125	Treelet	Drupe	0.23
<i>Phoebe lanceolate</i> Nees Nees	Lauraceae	PHOELA	2409	Understorey	Drupe	4.43
<i>Phoebe minutiflora</i> H.W. Li	Lauraceae	PHOEMI	319	Understorey	Drupe	0.47
<i>Phoebe puwenensis</i> Cheng	Lauraceae	PHOEPU	231	Lower canopy	Drupe	1.63
<i>Syzygium latilimbium</i> Merr. & L.M. Perry	Myrtaceae	SYZYLA	747	Understorey	Berry	5.340
<i>Syzygium oblatum</i> Roxb. Wall. ex Cowan and Cowan	Myrtaceae	SYZYOB	145	Understorey	Berry	0.66
<i>Syzygium rockii</i> Merr. & L.M. Perry	Myrtaceae	SYZYRO	333	Understorey	Berry	1.62
<i>Walsura robusta</i> Roxb.	Meliaceae	WALSRO	164	Lower canopy	Berry	1.52
<i>Walsura yunnanensis</i> C.Y. Wu	Meliaceae	WALSYU	156	Treelet	Berry	1.43
<i>Xanthophyllum siamense</i> Craib	Polygalaceae	XANTSI	506	Lower canopy	Drupe	1.58
<i>Xanthophyllum yunnanense</i> C.Y. Wu	Polygalaceae	XANTYU	96	Understorey	Drupe	0.64

**Appendix 2.** Species habitat association (by using torus-translation test) and distribution pattern of the 48 species in the 20-ha permanent plot of tropical seasonal rain forest in China. Topographical types include valley (slope < 27.1°; altitude < 765 m), hillside (slope > 27.1°; altitude < 765 m), hilltop (slope ≥ 27.1°, altitude ≥ 765 m, convexity > 0), high-gully (slope ≥ 27.1°, altitude ≥ 765 m, convexity < 0), high-plateau (slope < 27.1°, altitude ≥ 765 m, convexity > 0) and gap (with a total open area greater than 200 m<sup>2</sup>). “+” indicates positive correlation; “-” indicates negative correlation; See Appendix 1 for species codes.

Species code	Habitat association	Saplings	Large trees
ALPHHA	Hillside-	Aggregated	Aggregated
ALPHMO		Aggregated	Aggregated
ANTIJA		Aggregated	Aggregated
ANTIMO	Hillside+; High-plateau-;	Aggregated	Aggregated
ARDIQU	Valley-; Hillside-; High-plateau+	Aggregated	Aggregated
ARDISO	Hilltop-	Aggregated	Aggregated
BEILRB		Aggregated	Random
BEILRX	High-plateau-	Aggregated	Random
CANASU	High-gully-	Aggregated	Random
CANATO		Aggregated	Aggregated
CASTEC	Hillside-; High-plateau+	Aggregated	Aggregated
CASTHY	Hillside-; High-plateau+	Aggregated	Aggregated
CASTIN	Valley+; Hillside+; Hilltop-; High-plateau-	Aggregated	Aggregated
CASTMG		Aggregated	Aggregated
CASTMK	Hillside-; High-plateau+; Gap-	Aggregated	Aggregated
DIOSHA	Valley+; Hillside+; Hilltop-; High-plateau-	Aggregated	Aggregated
DIOSNI	Valley+; Hilltop-; High-plateau-	Aggregated	Aggregated
ELAEAU	Hillside-; High-plateau+	Aggregated	Aggregated
ELAEGL	Valley+; Hilltop-; High-gully-; High-plateau-	Aggregated	Aggregated
ELAERU	High-plateau-	Aggregated	Random
ELAEVA	Valley+; High-gully-	Aggregated	Aggregated
FICUAU		Random	Aggregated
FICUCH		Aggregated	Aggregated
FICUFI	Hillside+	Aggregated	Random
FICULA		Aggregated	Aggregated
GARCCO	Hillside-; High-gully-; High-plateau+	Aggregated	Aggregated
GARCLA	Hilltop+	Aggregated	Aggregated
GARCXA		Random	Random
HORSGL		Aggregated	Random
HORSPA	Hillside+; Hilltop-; High-plateau-	Aggregated	Random
KNEMFU	Gap-	Aggregated	Aggregated
KNEMGL	Valley+; Hillside+; High-gully-; High-plateau-	Aggregated	Aggregated
LITSBA	Hillside-	Aggregated	Aggregated
LITSDI	Valley+; Hilltop-	Aggregated	Aggregated
LITSGA	Hillside-; High-plateau+	Aggregated	Aggregated
LITSPA		Aggregated	Aggregated
LITSPI	Valley-	Aggregated	Aggregated
LITSVE	Valley-	Aggregated	Aggregated
PHOELA	Hillside-; High-plateau+	Aggregated	Aggregated
PHOEMI	Valley-; Hillside-; High-plateau+	Aggregated	Aggregated
PHOEPU	Valley-; Hillside-; Gap-	Aggregated	Random
SYZYLA	High-plateau-	Aggregated	Aggregated
SYZYOB		Aggregated	Aggregated
SYZYRO	Hillside-; High-plateau+	Aggregated	Aggregated
WALSRO	High-plateau-	Aggregated	Aggregated
WALSJU		Aggregated	Aggregated
XANTSI		Aggregated	Aggregated
XANTYU	Gap-	Aggregated	Random

**Appendix 3.**

Classification of associations at the tropical seasonal rain forest of China. Allocation of the three scales association of 112 species-species pairs based on the classification axes. Axis  $P$  is positive (negative) if there are on average more (less) pattern-

2 points at distance  $r_L$  (5 m, 30 m, 50 m) from pattern-1 points than expected without first- and second-order effects, and axis  $M$  is positive ( $L$  (negative) if the probability that a pattern 1 point has its nearest pattern-2 point within distance  $r_L$  is larger (smaller) than expected. 5-m scale (a); 30-m scale (b); 50-m scale (c).

